Bull Bot Surv India
Vol 28, Nos 1-4 pp 55-62, 1986

HONEY BEE — FLOWER RELATIONSHIP

M. C. SURYANARAYANA

Central Bee Research Institute, KVIC, Pune

ABSTRACT

Insects can be classified based on their food habits, as omnivorous, carnivorous, saprophagous and phytophagous. Obligatory phytophagy of the early insects might have led to the insect-plant relationship that is interdependent and evolutionarily very significant for both the partners. Leppik (1957, 1977) and Deodikar (1961) gave detailed accounts of the synagonistic relationship between flowering plants and insects and classified the flower forms into amorphic, haplomorphic, actinomorphic, pleomorphic, stereomorphic and zygomorphic types.

Insects show evolutionarily increasing trends in their body structure, physiology, behaviour and sensory perception as they changed in their food habits from a general phytophagy to anthophagy.

CO-EVOLUTION OF INSECTS AND FLOWERING PLANTS

The amorphic flower type is believed to be the precursor of the true flowers and perhaps was associated with the primitive insect forms like Coleoptera which fed on plant parts including the fleshy strobili. The chance feeding on the reproductive parts of the plants resulted in pollination and better reproduction in the plants. The nutritionally rich spores of the plants began to attract the spore-eating insects, which dispersed the spores in the process. The tropheclectic (food-searching) behaviour of insects, aided by their complex sensory mechanisms, directed new trends in floral evolution.

The true flowers developed with protective outer whorl of sepals, attractive inner petals and the spore-rich whorl of stamens followed by the carpels. These characters helped the spore-eating insects to locate their source of food in special organs of the plants they visited. The specialization in the flower structure exerted a reciprocal influence on the evolution of their insect visitors, which developed newer physical and sensory capabilities to help them locate their food sources.

The earliest known angiosperms possessed haplomorphic and actinomorphic flower types and were believed to have co-existed with a variety of insect orders including Coleoptera, Diptera and Hymenoptera.

The mutual inter-dependence of the anthophilous insects and entomophilous angiosperms hastened their co-evolution, and in the Tertiary period highly evolved insect groups are found associated with highly developed flower structures. By this time nectar was introduced as a food in the entomophilous flower syndrome. Pleomorphic flowers were found in several angiospermous groups of that period. Consequently, the flowering plants reproduced and spread rapidly in their populations in vast areas. Among the extant insects, the aculeate Hymenoptera, with their higher sensory capabilities emerged as predominent pollinators.

Anthophilous habit brought about changes in the insect biology, which include their diurnal rhythm, most of them feeding during the sunlight hours, stouter bodies, coupled with persistent appetites and boundless energy in pursuit of food (Brues 1972).

BEE FLOWERS

The first known fossil bees are of Eocene age, but at that time they were already quite specialized. Bees, entirely dependent on flowers for food could not have arisen before the appearance of the angiosperms. It is therefore believed that bees might have co-evolved during middle-Cretaceous period along with the then already dominant angiosperms (Michener 1974).

Apoidea, or the bees, are known to collectively visit more flowers than all other groups of anthophilous insects (Percival 1965). They show a high degree of adaptation to anthophily, and an increasing dependence on pollen and nectar for their development and growth. They provide their young with this food. They have branched hairs all over their body, and special structures on their legs to collect pollen. Their optical, olfactory and gustatory senses are well-developed. They can distinguish colours, shapes and scents of flowers and can learn the intricate floral structures and reach the concealed nectar. Further, they have developed time-sense and can forage for food as it is produced in the flowers (Kevan and Baker 1983). Bees can therefore be expected to have exerted selective pressures on the evolution of the flower types, which in the main were directed to (1) increase the complexity in colour, shape and structure of the flower, (2) reduce the number of floral parts and (3) produce and protect nectar.

Bee flowers are known to have all flower colours. Blue, purple, yellow and orange are common, which are within the range of colour perception of bees. The colours are deeper and pronounced than those of moth flowers, which are paler and generally white. Yellow which reflects ultraviolet is attractive to bees. Although red cannot be seen by most bees, the contrasting patterns made by a red flower with its background can be percoived. Similarly, ultraviolet, seen by bees, but not by human beings, is reflected by the petals of several flowers, particularly as nectar guides. The apparent colour pattern of flowers seen by humans, can for this reason, be quite different to the bees' eyes.

The flower shape or form is the unit, which the pollinator recognizes. This means that a flower-form seen by the pollinator is not necessarily a single flower. A capitulum of Asteraceae, or an umbel of Apiaceae is recognized by the pollinator as a flower-form. Even the compound inflorescences of *Poinsettia pulcherrima* or *Lagascea mollis* are single flower-forms to the pollinators.

An important evolutionary step in floral evolution was the development of form-number (Leppik 1955). The unlimited number of floral parts in the actinomorphic flower type has been reduced and 2-, 3-, 4- and 5-merous flowers developed which present characteristic floral patterns, called form-numbers (e.g., triangular in 3-merous flowers of Liliaceae, cross-shaped or pentagonal in 4- or 5-merous flowers of Brassicaceae and Rosaceae). Bees can recognise, learn and remember these form-numbers and can associate these with the source of food. These pleomorphic flowers are the general bee flowers. As the evolutionary trends in both the flowers and insects progressed, specific interrelationships developed, many examples of which can be seen in the modern angiosperms. In the flowers, stereomorphy, bilateral symmetry and finally zygomorphy have developed to cater to these species-specific associations. In stereomorphic flowers the trend was to locate nectaries in deep recesses of the flower, which discourage short-tongued insects. Bilateral symmetry demands a capability in the pollinator to distinguish this form from other types of food sources. The form-number lost its significance in the later stages of floral evolution and in zygomorphy it is conspicuous by its absence. Extreme cases of such associations are presented in Orchidaceae and flowers of species of *Ophrys* indeed resemble the females of certain species of wasps and bees and attract the males of these species (Percival 1965).

The olfactory sense of bees resembles that of man. Most of the bee flowers are sweet scented. Although odour of the flowers is an attractant to a variety of pollinators, the mimetic scents are often associated with beetles and flies and bee flowers have individualised scents associated with specific insects.

Bees are sensitive to pheromones that control their physiological processes. An interesting role of odour in bee-flower relationship is provided by species of *Ophrys* — aculeate Hymenoptera association. Kullenberg and Bergstroem (1976) showed that scolid and sphecid wasps, as also solitary bees *Andrena* and *Colleces* are attracted to species of *Ophrys* by specific chemicals which mimic pheromones of the female species of their pollinators. Chemical excitation plays a more important role in attracting the male insects than optical simulation, which remains as a secondary factor.

Bee flowers show complicated mechanisms of presentation of pollen and nectar. These ensure that the pollinators get the reward and others are discouraged. The spurred flowers of Geraniales or Ranunculaceae, papilionaceous flowers of Fabaceae, the lever mechanism in *Salvia* and other Lamiaceae are good examples.

A progressive trend can be seen to improve the quality of food produced in the bee flowers. While early angiosperms had large quantities of pollen serving as the only food to the pollinator, later flowering plants show a gradual reduction in the quantity of pollen and introduction of nectar as an attractive food.

Nectar, the food sought by most pollinators, varies in composition from purely sucrose-type, as in Ranunculaceae and Berberidaceae, to hexose-dominant type found in advanced families like Brassicaceae, Apiaceae and Asteraceae. An equal proportion of sucrose, fructose and glucose in the nectar is the most preferred type for bees and more or less similar nectar was reported in *Melilotus alba* (Furgala *et al.* 1958).

Pollen of anemophilous plants is rich in carbohydrates. Entomophilous flowers have protein-rich pollen, while several bee flowers like those of Asteraceae and Brassicaceae have pollen rich in proteins and lipids.

Evolution of floral structures and chemical composition of the food offered can be correlated with the sensory development of the particular plant pollinators (Leppik 1957, 1968).

A logical consequence of such selective pressures by bee flowers and their pollinators, on each other, is the development of exclusive and species-specific flower-pollinator associations. Some examples of such associations are the *Xylocopa* and Leguminales; Euglossine bees and orchids; *Peponapis* and *Cucurbita*, *Halictus nelumbonis* and *Nymphaea*; and *Emphor bombiformis* and *Hibiscus lasiocarpus*. Most of the bees have thus developed oligotropy, *i.e.*, foraging on a few related plant species, or monotropy, *i.e.*, foraging exclusively on a plant species.

Honey bees are social insects, with adult individuals of atleast two generations living together in a colony. An important aspect of the social behaviour is the collection and storage of food by the adults for feeding themselves or their young. This change in the feeding habit has brought about significant changes in the bee-flower relationship as observed in the fore-going discussion. A brief description of the biology of a honey bee colony will help in appreciating the honey bee-flower relationship.

BIOLOGY OF A HONEY BEE COLONY

Honey bees belong to the subfamily Apinae of the family Apidae. The stingless honey bees in the tribe Meliponini are abundant in the tropics. In India *Trigona* is the commonly found genus. *Trigona* builds nests in dark enclosures with a material made of wax, resin, propolis and mud. There are loosely clustered small elliptical cells for rearing their brood and similar but larger food pots in which pollen and honey are stored. True honey bees belong to the genus *Apis*. *A. mellifera,* the European honey bee and *A. cerana,* the Oriental honey bee are kept in boxes for honey production and other purposes. They construct several parallel combs in dark enclosures. There are two other common *Apis* species : *A. dorsata,* the rock bee or giant bee is the largest honey bee and *A. florea,* the little bee, is the smallest of the *Apis* species. Both these species build single combs in the open.

A colony of honey bees consists of generally one queen bee, and from a few to 60 thousand worker bees, which are sterile females. The queen bee is the mother of the colony and has the only function of laying eggs after mating. However, the pheromones produced by the queen bee control the behaviour and various functions of the worker bees, like brood-rearing and foraging. The workers too produce several pheromones, which help their team mates in communications, orientation to the hive, defense and in foraging. Worker bees in a colony exhibit a division of labour, the specific activity of a bee depending upon its age, physiological condition and requirement of the colony. Younger bees do various chores within the hive, while the older go out for foraging. An adult worker bee dies in the field engaged till the end in foraging activity. Nearly half of the worker bees in a colony, *i.e.,* about 30000 are foragers.

Reproduction of a honey bee colony is linked to the flowers of the locality serving as sources of forage. When supply of food is in plenty, generally in the spring, and particularly when lipid-rich pollen is available, bees initiate the process of reproduction, by rearing male bees. After this, some new queen bees are produced. When the daughter queens are ready for mating, the mother queen with about one-half of the worker population goes in a swarm out of the hive and establishes a new colony elsewhere. The old colony starts its normal activities as soon as one of the successful daughter queens returns to the hive after mating and starts egg-laying.

For a strong colony of *A. mellifera,* about 20 kilograms of pollen and 200 kilograms of honey are needed in a year. While pollen is collected, mixed with a little nectar and stored directly in the cells, the nectar collected from flowers undergoes chemical change by the action of the digestive enzymes of the bees. The dilute honey is then concentrated by removing water from it through fanning and setting up drying wind-currents within the hive. Honey contains about 40 per cent each of fructose and glucose and 5 per cent of sucrose. Nearly 20 per cent is accounted for by water in it. Honey is thus a super-saturated delicately balanced sugar solution. Due to its high sugar concentration, honey is antiseptic. Yeasts which are generally associated with nectars, cannot grow and deteriorate such super-saturated honey. Success of honey bees as a social organization is largely due to the evolution of honey as a stored high-energy food, used to feed themselves or their young during floral dearths and other adverse conditions.

From the available paleontological evidence, social bees existed at least as early as in the late Eocene and Oligomiocene. *Apis* species are known in early Miocene.

FORAGING BY THE HONEY BEES

It can be easily guessed that honey bees need food habits modified from those of other bees, in order to collect massive quantities of food. Although they are highly evolved and show the most advanced anthophilous features, they are not oligotropic. Their forage sources infact include several thousand flowering plant species. They are polytropic and collect their food from even anemophilous flowers and sometimes from outside the flowers. A typical example is offered by honey bees foraging on the leaf nectaries of *Hevea brasiliensis* (Suryanarayana 1980). Species of Poaceae like maize, millets and wild grasses, Arecaceae like *Phoenix, Borassus* and *Cocos,* Amaranthaceae and several other anemophilous plants are common sources of pollen. Similarly flowers of *Butea, Erythrina, Bombax* and *Dendrophthoe* with typical ornithophilous features are eagerly visited by honey bees for pollen and nectar. In the case of *Dendrophthoe,* pollen foragers learn to visit mature flower buds, which burst open as the bee alights on the tip of the perianth (Chandran and Suryanarayana 1970). The rich source of pollen is then systematically exploited by the bee.

In the tropical climates, honey bees face competition from a variety of insects. At the same time, the food sources are unlimited and varied. Availability of food however is subject to a number of environmental, edaphic and other factors. Survival and development of honey bee colonies depends on the adaptation of the bees to the varying circumstances, and successful exploitation of the available food. Honey bees show temporal adjustments for foraging and exhibit other behavioural features which allow advantageous resource sharing with other insects. A few examples of the adaptive behaviour of honey bees while foraging on various flowering plants are given here. These are the observations made in the experimental apiaries of the Central Bee Research Institute in different parts of the country.

Honey bees exhibit a remarkable ability to discriminate and learn intricate floral mechanisms. The papilionaceous flowers of lucerne (*Medicago sativa* Linn.) need to be 'tripped' to effect pollination, which alone provides the reward for the pollinators. Heavier insects like the leaf-cutter bee can trip lucerne flowers, while the lighter *Apis-cerana* normally cannot. Several foragers do, however, succeed after some persistent efforts to trip the flowers and reach the nectar. A successful forager was found to learn this technique, for, in the subsequent visits, the tripping took place quite quickly. Shelar and Suryanarayana (1983) found that *A. cerana* contributed to 80% of the yield in lucerne which indicates the relative success of the foragers in tripping.

Floral dearth periods are critical for the survival of bee colonies. During such dearths, they are observed to forage on any suitable food source. Even dilute nectar, not collected in normal periods, are sought eagerly. Foraging during such dearths on *Synadenium grantii* Hook. f. having open disc shaped flowers with annular exposed nectaries, presents an example of honey bees' ability to adapt to the abnormal environmental situations. In the *Synadenium* flowers, the exposed nectar crystallizes into sugar in the form of a ring around the disc. Nectar collectors visit initially a source of water in their foraging trip after which they visit the *Synadenium* flowers. The water collected earlier is regurgitated and mixed with the sugar crystals. The solution thus made is then imbibed by the forager (Diwan and Rao 1969).

Safflower (*Carthamus tinctorius* Linn.) an originally entomophilous species, has adopted itself to the insect-free environments by self-compatibility. An early dehiscence of anthers, before the elongation of the style enables autodispersal of pollen on to the stigma of the same flower. Ramachandram and Rangarao (1984) observed genetic difference in the time of anther dehiscence in safflower. Late dehiscence delays self-pollination and makes the flowers dependent on an agent for pollination. *Apis cerana* is found to help in cross pollination as they forage on the flowers just as the anther dehiscence take place. This helps in pollen dispersal between flowers (Deshmukh *et al.* 1984).

The flowers of *Carthamus* are yellow and change with age to orange and red, which indicates successful fertilization of the flowers. Orange or red flowers no longer produce nectar. Honey bees can notice the colour change and are found to consistently avoid visiting the old flowers. This saves energy for the bees and increases their efficiency in pollination.

The flowers of cardamom (*Elettaria cardamomum* Maton) are self-fertile, but have the single anther situated below the stigma. The pollen is sticky and cannot be transferred to the stigma without an agent. Cardamom flowers during May-October coinciding with the heavy monsoon period. In these conditions, water surrounding the flowers may help in its pollination. However, *Apis cerana* was found to be the only pollinator, which with its characteristic movements in pollen foraging transferred pollen from the anther to the stigma. Chandran *et al.* (1980) found that honey bees contributed to a significant increase in the yield of cardamom.

Sesame (*Sesamum indicum* Linn.) presents pollen nototribically. However, *Apis cerana* adapts itself to the quicker and more efficient sternotribic collection. For collection of pollen, the forager alights on the limb of the flower and as it enters the corolla tube, turns over, so that the ventral side of the body faces up and touches the anthers. In this position it bites the anthers and gets the pollen on the mouth parts and ventral part of the thorax. The bee then retraces slowly out of the tube and hovering above the flower packs the pollen (Mohanarao *et al.* 1981).

Sesame is entomophilous but adapted itself to self fertility due to its cultivation in pollinator-free environments. The stigma is receptive early in the morning. If cross pollination does not take place in the morning due to absence of pollinators, self pollination mechanism becomes operative. *A. cerana* visiting the flowers early in the morning contributes to cross-pollination.

The foraging rhythm in honey bees is well-adapted to the availability of food. Although normally diurnal, honey bees can forage in the nights, if there is sufficient moonlight. Species of *Terminalia, Lagerstroemia* (Dyer 1985) and *Careva* (Diwan and Salvi 1965) were observed in Karnataka to be actively visited by the honey bees in moonlit nights.

Bees try to collect pollen when it is freshly produced in the flowers. Being moist this facilitates its packing by the bees. By adjusting to this timing honey bees also successfully compete with other insects in collection of food. Fresh pollen remains viable while the bee disperses it on to other flowers where the stigmas are receptive. This behaviour makes the honey bees efficient pollinators.

Sources of nectar rich in sugars and pollen rich in proteins and lipids are generally preferred by honey bees. A sugar-rich nectar conserves the forager valuable energy. Nectars of *Schefflera, Hevea* and *Nephelium* (Nair 1983) are eagerly sought by *A. cerana* because of their high sugar content. In *Hevea* (Nair and Wakhle 1983), *Schefflera* and *Thelapaepale ixiocephala* Bremk. (Wakhle *et al.* 1981), which are important honey plants, the nectars are fructose and glucose dominant, and are technically honeys. For the bees these nectars do not involve any action of digestive enzymes, and are beneficial as they enable conservation of bees' energy.

Foraging honey bees are either specialist pollen or nectar collectors, although they change over from one to the other according to the need of the hive and availability of food on the plants. They usually select a plant species for pollen or nectar collection, depending upon the quality and quantity of the food offered. Once a species is selected, the successful forager communicates the information on the food source to its hive mates by characteristic dances. The information given to the potential foragers consists of the direction, distance, quality and quantity of food available. Other foragers partake some food brought in by the successful forager and follow its directions. They can locate the food sources without fail, even when other sources come in their way. This behaviour enables the colony to exploit a forage source to the maximum, and is a result of bees' innate response to external stimuli. In view of this, bees show the behaviour of floral constancy. The foraging activity is restricted to a single plant species, as long as it provides food. Floral constancy in bees enables a beekeeper to get unifloral or single-source honeys. This behaviour is the basis for the efficiency of honey bees as crop pollinators.

Foraging is controlled by several pheromones produced within the colony and by similar chemicals of the food in the flowers. Pollen collection, for example, is instigated by a brood pheromene in a normal colony, in which all the usual activities are controlled by the queen substance. A lipid-rich pollen source stimulates brood rearing. Brood is reared when the queen bee lays eggs, which is possible when the young nurse bees produce and feed the queen bee with royal jelly. Royal jelly is produced by the nurse bees when they eat large quantities of pollen. Increased brood production automatically results in an increased pollen foraging. The number of pollen foragers is thus proportionate to the amount of pollen available in the flowers.

The stimulus received by a potential forager enables it to reach the general area of the floral source. The specific odour of the source stimulates the olfactory sense and helps in orientation to the source. The optical stimuli in the form of flower size, shape and colour pattern operate when the forager comes closer to the source. The gustaroy and tactile stimuli on the flower instigate the bee to exhibit the typical behaviour of scrabbling, crawling and biting the anthers. The pollen on the hairy body instigates the cleaning and packing process (Free 1967). A satiated bee is similarly instinctively oriented to go to its colony for dislodging and storing the food.

One of the conditions for brood rearing is also the availability of comb space for the queen to lay eggs. Older bees in the hive undertake comb building when their wax glands become active. Wax is produced by consuming large quantities of honey. This means that nectar foragers should be active and bring in nectar in adequate quantities.

Foraging behaviour, like all other activities of honey bees, results from their innate — and therefore, unavoidable — responses to environmental stimuli (Doull 1970). Honey bees have therefore innate capabilities to adapt to any foraging situation, converting it into an advantage to the colony. An understanding of the inter-relationship between honey bees and flowering plants, helps in their efficient utilization for production of honey and other economic materials as also for ensuring and improving crop production through efficient pollination.

REFERENCES

BRUES, C.T. Insects, Food and Ecology. Dover Publ. Inc., New York. 1972.

CHANDRAN, K. AND M. C. SURYANARAYANA. A note on entomophily in *Dendrophthoe falcata* and its usefulness to the Indian honey bee. *J. apic. Res.* 9 45-47. 1970.

—— P. RAJAN, D. JOSEPH AND M.C. SURYANARAYANA. Studies on the role of honey bees in the pollination of cardamom. *Proc. 2nd.Int. Conf. Apic. Trop. Climates.* Indian Agricultural Research, New Delhi (1983) : 497-504. 1980.

DEODIKAR, G.B. Some aspects of bee botany. In Prof. S.P. Agharkar Commemoration Volume, MACS Research Institute, Pune, 61-78. 1961.

DESHMUKH, A.K., G. MOHANARAO AND A.D. KARVE. Studies on the effect of honey bee pollination on the yield of safflower. *Indian Bee J.* 46. 1984.

DIWAN, V.V. AND S.R. SALVI. Some interesting behavioural features of *Apis dorsata* Fabr. *Ibid.* 27: 52. 1965.

DOULL, K.M. An analysis of bee behaviour as it relates to pollination. *In The Indispensable Pollinators. Rep. IX Pollination Conf.,* Hot Springs, Arkansas, 5-18. 1970.

DYER, F.C. Nocturnal orientation by the Asian honey bee. *Apis dorsata. Anim. Behav.* 33, 1985.

FREE, J.B. Factors determining the collection of pollen by honeybee foragers. *Ibid.* 15 : 134-144. 1967.

FURGALA, B., T.A. GOCHNAUER AND F.G. HOLDAWAY. Constituent sugars of some northern legume nectars. *Bee Wld.* 39 : 203-205. 1958.

KEVAN, P.G. AND H.G. BAKER. Insects as flower visitors and pollinators. *Ann. Rev. Entomol.* 28 407-453 1983.

KULLENBERG, B. AND G. BERGSTROEM. The Pollination of *Ophrys* orchids. *Bot. Notiser* 129(1) : 11-20. 1976.

LEPPIK, E.E. How bees recognize numbers. *Am. Bee J.* 95 : 472-473. 1955.

—— Evolutionary relationship between entomophilous plants and anthophilous insects. *Evolution.* 11 : 466-481. 1957

—— Directional trend of floral evolution. *Acta Biotheoretica.* 8(1) : 1-16. 1968.

—— Floral Evolution in Relation to Pollination Ecology. Today & Tomorrow's Printers and Publishers, New Delhi. 1977.

MICHENER, C.D. The Social Behaviour of the Bees. Bilknap Press of Harvard University Press, Cambridge. 1974.

MOHANARAO, G., M. LAZAR AND M.C. SURYANARAYANA. Foraging behaviour of honey bees in Sesame *(Sesamum indicum* L.). *Indian Bee J.* 43 : 97-100. 1981.

NAIR, K. SHAKUNTALA. Evaluation of importance of Litchi as a nectar source. *Ibid.* 45.1983.

—— AND D.M. WAKHLE. A qualitative and quantitative study of foliar nectar of rubber tree. *Ibid.* 45. 1983.

PERCIVAL, MARY, S. Floral Biology. Pregamon Press, Oxford. 1965.

RAMACHANDRAM, M. AND V. RANGARAO. Seed setting as influenced by difference in anther dehiscence in safflower. *Indian J. Genet.* 44 113-116. 1984.

SHELAR, D.G. AND M.C. SURYANARAYANA. Effect of Pollination by honey bee *(Apis cerana indica* Fabricius) on the yield of lucerne. *Indian J. Agric. Sci.* 53 : 190-191. 1983.

SURYANARAYANA, M.C. The rubber tree *(Hevea brasiliensis)* — an important nectar source in the tropics. *Proc. 2nd.Int. Conf. Apic. Trop. Climates,* Indian Agricultural Research Institute, New Delhi 1983, 656-658. 1980

WAKHLE, D.M., K. SHAKUNTALA NAIR AND B. RAMESH. Sugar composition in nectars of certain plants. *Indian Bee J.* 43 : 6-8. 1981.